SPATIAL AND TEMPORAL DYNAMICS OF A PURPLE MARTIN PRE-MIGRATORY ROOST

KEVIN R. RUSSELL^{1,2,3} AND SIDNEY A. GAUTHREAUX, JR.¹

ABSTRACT.—We used simultaneous WSR-88D radar (NEXRAD) and direct visual observations to investigate the spatial and temporal dynamics of a Purple Martin (*Progne subis*) pre-migratory roost in South Carolina. The timing of mass flights of martins from and to the roost was related to levels of ambient light. Each morning, the birds first departed approximately 40 min before sunrise independent of date, with peak departures occurring about 10 min before sunrise. The time of evening flights was more variable, but peak movement of birds into the roost consistently occurred at sunset. Purple Martins exited the roost in organized, annular departures (360°) that were visible on radar up to 100 km away from the roost, but returned to the roost over an extended period in scattered flocks. During morning departures we recorded flight speeds up to 13.4 m/s. Radar echoes corresponding to martin flights were recorded farther from the roost, and flights from and to the roost appeared to be displaced by winds aloft. At the peak of the roosting season in late July, the total roost population was estimated to be at least 700,000 birds. *Received 18 Aug. 1998, accepted 5 Feb. 1999*.

Purple Martins (Progne subis) are neotropical migratory swallows that breed across North America (Brown 1997, AOU 1998). In eastern North America, Purple Martins are conspicuous colonial nesters that almost exclusively are dependent on man-made nesting houses. As a result, martin breeding biology and behavior have been the focus of considerable study (see Brown 1997). After the fledging period eastern populations of Purple Martins often congregate in distinctive nocturnal roosts that may reach concentrations of 100,000 or more as a prelude to fall migration (Brown 1997). From late June through August or early September these assemblages engage in two mass movements daily: a morning exodus from the roost for aerial foraging and an evening return (Allen and Nice 1952). Although the existence of these large pre-migratory roosts is well documented (e.g., Bent 1942, Allen and Nice 1952, Anderson 1965, Brown and Wolfe 1978, Rogillio 1989, Russell et al. 1998), little quantitative data are available concerning their spatial and temporal dynamics.

Studies of communal roosts may be limited by the inability to collect data at appropriate spatial and temporal scales (Caccamise et al.

³ Corresponding author;

1983, Russell et al. 1998). Locating roosts often is labor-intensive (see Caccamise and Fischl 1985, Komar 1997). Even when roost locations are known, visual surveys alone provide only limited data on the spatial extent and direction of roosting flights (Brown and Wolfe 1978), and the time of movements (e.g., pre-dawn flights) may limit visual observations (Russell and Gauthreaux 1998). Recently, we developed methods for using the National Weather Service's new doppler weather surveillance radar, the WSR-88D or NEX-RAD to locate and study communal roosting assemblages (Russell and Gauthreaux 1998, Russell et al. 1998). In this study, we provide quantitative data on the spatial and temporal dynamics of a pre-migratory roost of Purple Martins in South Carolina using simultaneous WSR-88D radar and direct visual observations. Our specific objectives were to document the daily timing and spatial pattern of roosting flights, flight directions and speeds, the influence of weather conditions on roosting flights, and seasonal changes in roost population size.

METHODS

Study area.—Our study site was a Purple Martin roost on Lunch Island (34° 03' N, 81° 18' W), a 5-ha island located in Lake Murray, near Columbia, South Carolina (Russell and Gauthreaux 1998: fig. 2). We conducted visual surveys from a peninsula on the shoreline of the lake, approximately 3 km south of the roost. Radar data were collected at the National Weather Service Office, Columbia Metropolitan Airport, 28 km southeast of the roost site. A detailed description

¹ Dept. of Biological Sciences, Clemson Univ., Clemson, SC 29634.

² Current address: Willamette Industries, Inc., P.O. Box 488, Dallas, OR 97338-0488.

E-mail: krussell@wii.com

of the study area is provided in Russell (1996) and Russell and Gauthreaux (1998).

Survey methods.-We conducted timed visual surveys of roosting flights 5 days per week from 30 June to 27 August 1995. We originally conducted morning surveys from 05:50 to 06:50 EST, but extended them to 07:30 when the duration of departures lengthened in late July. Evening surveys were conducted from 19: 15 to 21:15 throughout the study. During each visual survey, we recorded the numbers and flight directions of individual martins as they passed over a natural circular opening (24 m diameter; 48° angle of observation) in the forest canopy, using methods described by Lowery and Newman (1963) and applied to WSR-88D radar by Russell and Gauthreaux (1998). We identified martins in flight by their distinctive profile, behavior, and vocalizations (Brown 1997). The presence of other roosting species was negligible during the study (Russell 1996). When both numbers and flight directions could not be accurately recorded, we (1) assigned directions to flocks, or (2) only made counts for many of the birds. During surveys we also made incidental observations of the roost site with a $30 \times$ spotting scope and recorded general weather conditions. We later obtained detailed local climatological data (LCD) from the National Weather Service Office at the Columbia Metropolitan Airport.

Immediately after each visual survey we visited the National Weather Service Office and acquired WSR-88D radar images that coincided with our surveys, except for eight mornings when weather conditions obscured martin flights on radar. Evening flights of Purple Martins typically failed to produce recognizable patterns on the WSR-88D (Russell and Gauthreaux 1998); thus we present no radar data on evening arrivals. We collected base reflectivity images to monitor flights of martins in the proximity of the roost and composite reflectivity images to track flights over a wider geographic area (Russell and Gauthreaux 1998). We also collected several radial velocity images to determine directions and speeds of each mass flight. We recorded radar images by taking a 35-mm color slide exposure of each image as it was displayed on a monitor at the radar site. Detailed descriptions of the WSR-88D, radar images, and our survey methods are provided in Russell and Gauthreaux (1998).

Analyses.—We examined the timing of roosting flights by recording the beginning, end, duration, and peak of each mass flight from both the radar and visual data (Russell and Gauthreaux 1998). We also examined temporal changes in the numbers of departing and arriving birds by pooling our visual counts into 15-min totals based on our timed surveys (Russell 1996). We characterized the spatial patterns of roosting flights by examining the origin, timing, intensity, number, and spatial distribution of echoes from each radar image of the roost area (Russell and Gauthreaux 1998). We measured the maximum spatial extent of each mass flight by relating echoes created from the leading edge of the flight to landmarks depicted on the radar (e.g., county boundaries). We excluded mornings when regional precipitation or spurious ground echoes obscured the maximum extent of flights.

We pooled visual flight tracks of individual birds so that peak movement from or to the roost was not divided artificially (Russell 1996); then examined temporal changes in flight directions using circular statistics (Zar 1984). We scored directions and speeds of each mass flight directly from the radar images (Russell and Gauthreaux 1998).

We used univariate correlation and stepwise multiple regression to examine the influence of weather conditions on roosting flights. Daily climatological data (mean, 04:00, 07:00, 19:00) included temperature, dew point, total precipitation, atmospheric pressure, surface wind speed, visibility, and cloud cover. Variables initially entered or left the stepwise models at P = 0.1. We examined the influence of winds aloft on morning departures by scoring the modal azimuth of annular displacement (relative to the roost site; Eastwood et al. 1962) and regressing these values against the corresponding direction of geostrophic winds aloft (1000 m above the ground or 900 mb; Riehl 1972) at 07:00.

The total roost population (TRP) represents the estimated daily sum of all birds at the roost (Caccamise et al. 1983). Based on a preliminary examination of the radar data, we assumed that departures and arrivals of Purple Martins were omnidirectional at approximately equal densities. Our visual sample area was 0.47° or 1/766 of the circumference around the roost at a distance of 3 km. Thus, we calculated separate morning and evening TRPs by multiplying the total count for each movement by 766 (Russell 1996) and examined changes in roost size. We used univariate correlation to investigate relationships between our morning and evening counts, and patterns of flight with time and date. We used JMP 3.1 (SAS Institute 1995) on an IBM computer for all analyses with probability values P < 0.05 recognized as significant and means reported ± 1 standard deviation (SD) unless otherwise noted. We standardized all survey times by converting to minutes before or after sunrise or sunset (as given by the National Weather Service Office in Columbia, South Carolina).

RESULTS

Timing of flights.—We detected the initiation of mass departures as a single radar echo corresponding to the location of the roost. Time of initial departure from the roost averaged 41.4 \pm 4.0 (SD) min before sunrise (range 31–48 min) and was independent of date ($r^2 = 0.02$, P > 0.05, n = 32; Russell and Gauthreaux 1998). Time of peak departure also was independent of date ($r^2 = 0.06$, P > 0.05, n = 32). Mean duration of morning departures (interval from first radar echo to last bird observed visually) was 67.9 \pm 12.2 min (range 49–101 min) and was positively

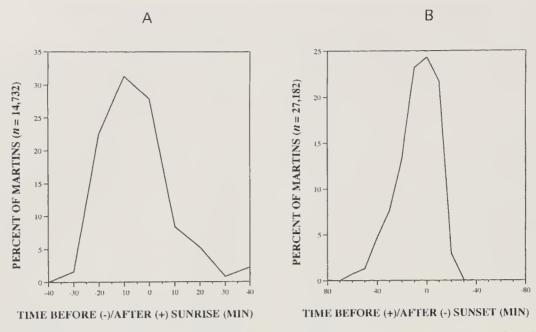


FIG 1. Changing numbers of roosting Purple Martins during visual counts of (A) morning departures and (B) evening arrivals, by time before and after sunrise or sunset.

related to the number of birds counted exiting the roost ($r^2 = 0.60$, P < 0.001, n = 32).

Changes in the numbers of Purple Martins observed departing the roost were related to the time of sunrise. Because some birds first departed in darkness, changes in the percentage of birds we observed 40-30 min before sunrise reflected their increased visibility in the morning sky rather than actual numbers aloft (Fig. 1A). Corresponding radar data indicated that, on average, the movement of most birds from the roost began 20.4 \pm 4.6 min before sunrise, when sufficient light was available for accurate visual counts (Russell and Gauthreaux 1998). The number of birds departing from the roost consistently peaked about 10 min before sunrise, then steadily declined over the next 40 min (Fig. 1A). We occasionally observed a small, secondary increase in the number of birds departing from the roost as late as 30-40 min after sunrise (Fig. 1A).

Purple Martins first returned to the roost an average of 59.8 \pm 13.5 min before sunset (range 35–84 min), and the last birds entered the roost 2–24 min after sunset ($\bar{x} = 15.5 \pm 5.9$ min). We found a weak negative relationship between the time that the last birds were observed entering the roost and date ($r^2 = 0.23$, P = 0.0033, n = 36), but not for the time of peak movement into the roost ($r^2 = 0.07$, P > 0.05, n = 36). Mean duration of observed evening arrivals at the roost (71.4 \pm

15.2 min, range 43–103 min) was not related to our visual counts ($r^2 = 0.05$, P > 0.05, n = 36), but we detected a negative relationship between the duration of evening flights and date ($r^2 = 0.71$, P < 0.001, n = 36).

Numbers of Purple Martins returning to the roost increased 50–30 min before sunset (Fig. 1B). At about 30 min before sunset, the number of arrivals increased rapidly until peaking at sunset (Fig. 1B). After sunset, numbers aloft declined rapidly and ceased by 24 min after sunset, and always before complete darkness.

Spatial pattern of flights.-Each morning until the peak of the roosting season, Purple Martins departed en masse from the roost in all directions (360°). These omnidirectional departures first were visible on radar as a roughly circular mass of echoes that extended across Lake Murray (Russell and Gauthreaux 1998: fig. 3). As departures continued, an expanding ring or annulus was seen on radar as the departing birds extended across the landscape directly away from the roost (Russell and Gauthreaux 1998: fig. 4). The maximum daily extent of flights we could detect on radar averaged 77.9 \pm 14.1 km (range 50–100 km, n = 20; Russell and Gauthreaux 1998): We found no relationship between the maximum distance of flights and date ($r^2 = 0.02$, P >0.05, n = 20) or our morning counts ($r^2 =$ 0.01, P > 0.05, n = 20). Beginning 12 August we observed on radar that more birds departed south than other directions; by 18 August birds only departed to the south and after 26 August we no longer observed departures on radar.

In the evening, Purple Martins arrived at the roost in sporadic, loosely organized flocks. The birds flew over the observation point at tree-top height (ca 18–25 m) and then flew down to just above the lake's surface, usually below the radar beam (Russell and Gauthreaux 1998). After reaching the roost the birds remained aloft in a growing mass that circled high over the island counter-clockwise until a final, spiraling entry into the roost at sunset.

Flight directions and speeds.—During morning departures, the Purple Martins we observed visually were consistently and significantly (P < 0.001) oriented to the south. The mean direction (\pm 95% confidence interval, vector length, angular deviation) of martins at 40–21 min before sunrise was 180° (2°, 0.953, 18°); at 20-1 min before sunrise was 184° (3°, 0.922, 23°); at 0–20 min after sunrise was 183° (4°, 0.884, 28°); at 21-40 min after sunrise was 182° (4°, 0.885, 28°); and at 41-60 min after sunrise was 190° (3°, 0.931, 21°). The radar images also showed the birds flying in a southerly direction over the observation point, consistent with an omnidirectional departure from the roost. Radar images of velocity that we acquired on 32 mornings showed that flight speeds of the departing birds ranged from 10.8-13.4 m/s (see figure 5 in Russell and Gauthreaux 1998).

We observed distinct changes in the orientation of Purple Martins during evening flights to the roost. The mean direction of martins at 90-71 min before sunset was 141° (90°, 0.364, 65°) and not significant (P > 0.05). During this time we often observed birds feeding in small flocks and flying away from the roost. As the time of sunset approached, however, the mean direction of martins at the observation point became significant (P < 0.001) and increasingly oriented towards the northeast, but still east of the roost (azimuth = 10° from observation point). The mean direction of martins at 70-51 min before sunset was 93° (18°, 0.318, 67°); at 50-31 min before sunset was 73° (14°, 0.399, 63°); at 30–11 min before sunset was 57° (9°, 0.590, 52°); at 10 min before to 9 min after sunset was 54° (5°, 0.836,

33°); and at 10–29 min after sunset was 53° (4°, 0.843, 32°).

Weather conditions and roosting flights.— Purple Martins first departed the roost earlier relative to sunrise with higher atmospheric pressure, surface wind speed, and relative humidity, but later relative to sunrise with increased cloud cover (stepwise multiple regression: $R^2 = 0.66$, P < 0.001, n = 32). Of these variables, atmospheric pressure was the most important and the only significant univariate relationship ($r^2 = 0.20$, P = 0.0068, n = 32). We also found a significant relationship between the duration of morning departures and atmospheric pressure (stepwise multiple regression: $R^2 = 0.29$, P < 0.001, n = 32).

Purple Martins were detected on radar farther from the roost on days with increased cloud cover or decreased visibility at 07:00 (stepwise multiple regression: $R^2 = 0.61$, P < 0.001, n = 20), although univariate analysis indicated a significant relationship only for cloud cover ($r^2 = 0.35$, P = 0.0063, n = 20). Mass departures from the roost also appeared to be displaced by winds aloft. Azimuthal wind direction was strongly related to the modal direction of annulus displacement ($r^2 = 0.76$, P < 0.001, n = 20).

Arrival of the first birds over the observation point was not related to any of the weather variables, but arrival of the last martins at the roost occurred earlier relative to sunset on days with more cloud cover and later in the season (stepwise multiple regression: R^2 = 0.40, P < 0.001, n = 36). Univariate analysis also indicated a significant relationship for cloud cover: $(r^2 = 0.13, P = 0.0275, n = 36)$. Maximum temperature, atmospheric pressure, and surface wind speed at 19:00 were identified by stepwise regression as significant predictors of the duration of evening flights (R^2 = 0.89, P < 0.001, n = 36), although no variable was significant when subjected to univariate analysis.

Seasonal changes in total roost population.—Despite fluctuations in the daily number of departing ($\bar{x} = 368.3 \pm 201.9$ SD, range 29– 916, n = 14,732 birds) and returning ($\bar{x} =$ 755.1 \pm 548.9 SD, range 108–2,531, n =27,182 birds) martins, the roosting population exhibited a seasonal pattern of growth and decline (Fig. 2). On the first morning census of 3 July we counted only 172 birds over the ob-

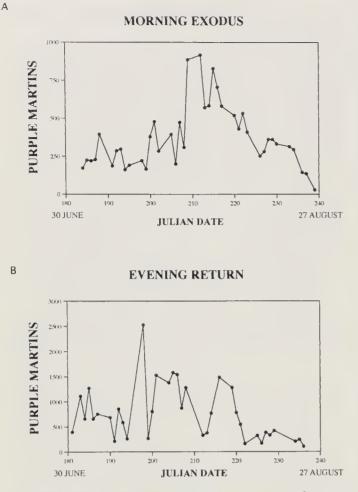


FIG 2. Seasonal changes in visual counts of roosting Purple Martins during (A) morning departures and (B) evening arrivals.

servation point yielding an estimated total roost population (TRP) of 131,752 birds, but on 31 July we counted 916 birds, yielding a peak morning TRP of 701,656 birds. On the last morning census (27 August), we counted only 29 birds (TRP = 22,214). Although evening counts usually were higher than morning counts, numbers of birds returning to the roost also followed a pattern of increase and decline (Fig. 2). The first (30 June), peak (17 July), and last (27 August) evening counts yielded TRPs of 301,804 birds, 1,938,746 birds, and 0 birds, respectively. However, the peak morning count occurred two weeks after the peak evening count and morning counts were not related to evening counts from the previous night (r^2 = 0.001, P > 0.05, n = 32) or the same night $(r^2 = 0.01, P > 0.05, n = 32).$

DISCUSSION

Timing of flights.—Our observations indicate that flights of Purple Martins from and to pre-migratory roosts are related to levels of ambient light. Purple Martins (Brown and Wolfe 1978, Oren 1980, Hill 1988), Crag Martins (*Ptyonoprogne rupestris*; Elkins and Etheridge 1974), and other species of swallows (Rudebeck 1955, Loske 1984, Skutch 1989, Komar 1997) have been shown previously to enter and exit roosts in response to changing intensities of light. Although endogenous factors likely are a significant influence on the timing of departures and arrivals of birds at roosts (Aschoff 1967), cueing on changing light levels has been suggested as a selective advantage for maximizing time available for feeding (Eastwood et al. 1962, Summers and Feare 1995).

The timing of evening flights was less predictable than morning departures and appeared to be related to date. Across a season the departure or arrival times of the first and last birds at roosts may show greater variation than peaks of departure or arrival (Summers and Feare 1995). In our study, more variation was associated with the times martins first arrived in the vicinity of the roost than when flights were terminated, as was reported previously for other roosting species (Eastwood et al. 1962, Meanley 1965, Bünning 1973, Krantz and Gauthreaux 1975). We suggest that relationships between date and the timing of evening arrivals of martins are related mostly to the large variation associated with these flights.

Spatial pattern of flights.—As with other roosting species (Harper 1959, Eastwood et al. 1962), the omnidirectional departures of Purple Martins that we observed on radar were associated with daily feeding flights (Russell 1996). In contrast, directionally biased patterns of flight on radar are often associated with migration departures (Harper 1959, Richardson and Haight 1970). The strong southerly bias in the annulus and its eventual disappearance during the latter part of August, in conjunction with our declining visual counts, marked increasing fall migration departures and eventual abandonment of the roost.

Among our more surprising results was the long distances Purple Martins flew from the roost. Prior to our study, it was believed that the birds foraged within 10–15 km of the Lake Murray roost (J. Cely, pers. comm.). Brown and Wolfe (1978) suggested that Purple Martins may travel as far as 48 km from pre-migratory roosts during the day while feeding. Our radar data clearly showed that birds regularly flew almost 80 km and occasionally as far as 100 km from the roost. If the large population size of the roost and thus foraging competition (Caccamise et al. 1983, Summers and Feare 1995) was responsible for the flight distances we observed, a significant relationship should have emerged between the extent of departures and changes in TRP, but it did not. In fact, some of the longest flights occurred early in the season, when TRP was relatively small. Because we did not track individuals, we do not know the ultimate destination of the birds or whether all departing individuals returned the same evening.

Flight directions and speeds.-In marked contrast to the uniform departures of Purple Martins, we observed high variability in the flight tracks of birds arriving at the roost. Even during the peak of arrivals, mean flight direction of the birds was east of the roost. This directional bias and our own incidental observations indicate that Purple Martins return to the roost via specific flight corridors. Use of preferred flight lines often is associated with evening movements to roosts (Eastwood et al. 1962, Meanley 1965, Skutch 1989). After arriving at the roost the birds assembled in a high, circling mass before a final entry at sunset. This pattern is very similar to the phases of "staging" or pre-settling behavior (initial aimless flight, formation of a tight flock near the roost, final descent; Loske 1984) previously described for Progne spp. (Brown and Wolfe 1978, Oren 1980, Hill 1988) and other genera of roosting swallows (Bent 1942; Loske 1984, 1986; Skutch 1989, Komar 1997). Flight speeds of departing Purple Martins we recorded on radar (10.8-13.4 m/s) were similar to those reported by Evans and Drickamer (8.45-11.09 m/s; 1994) and Southern (12.1 m/s; 1959).

Weather conditions and roosting flights.— Because Purple Martins apparently respond to some threshold level of ambient light for the cueing of flights from and to the roost, the timing of these movements should vary with daily differences in light levels caused by changing cloud cover (Richardson 1978, Elkins 1983). In our study, cloud cover and atmospheric pressure were the most important weather conditions explaining variation in the

timing of roosting flights. Increasing or decreasing light levels reach a given intensity later or earlier, respectively, on days with overcast conditions compared to clear days. Atmospheric pressure is often inversely correlated with the amount of cloud cover (Riehl 1972). The inclusion of other variables into the stepwise models also may have resulted from intercorrelations with cloud cover, atmospheric pressure, or date (Richardson 1978). Because these weather variables were highly intercorrelated, the most that can be assumed is that the birds responded to some aspect of the weather that was interrelated with the significant variables (Richardson 1978). Thus, we view our results as a preliminary explanation of variation in the flight behaviors of roosting Purple Martins, rather than representing causal mechanisms.

Finlay (1976) observed the influence of cloud cover on Purple Martins during the nesting season; the birds departed from nests earlier on clear days than on cloudy days. Also, Elkins and Etheridge (1974) found that Crag Martins returned to roosts up to 2.5 h earlier on overcast or cloudy days. The influence of cloud cover on the extent of martin roosting flights may in part be related to the aerial foraging habits of the birds (Elkins 1983). In two studies of Purple Martin food habits (Spice 1972, Walsh 1978), the intake of airborne insects was negatively correlated with cloud cover. Cloudy weather also was shown to reduce the amount and type of airborne insects taken by Brown-chested Martins (Phaeoprogne tapera) in Venezuela (Turner 1984). Additionally, Finlay (1976) reported that during overcast conditions martins appeared to spend more time away from nests, presumably searching for food. It is possible that cloudy conditions forced roosting Purple Martins to travel longer distances in search of prey (Elkins 1983).

Our radar observations that winds aloft displaced the annular departures of Purple Martins indicate that the birds continued to fly with constant headings and speeds, apparently making no correction for drift in spite of their presumed knowledge of the local topography. Similar radar observations were made by Eastwood et al. (1962) of wind displaced departures of European Starlings (*Sturnus vulgaris*) from roosts.

Seasonal changes in total roost population.-The overall increase in TRP through the end of July likely reflects recruitment of local and regional populations after the fledging period (Brown 1997). Although Purple Martins are colonial breeders they nest asynchronously (Brown 1997), and in South Carolina clutches have been observed as early as 11 April and as late as 19 June (Post and Gauthreaux 1989). Thus, it is not surprising that increases in TRP during July occurred gradually. The influx of birds at the roost also occurred too early in the season to be significantly influenced by migration. However, subsequent declines in TRP and changes in flight patterns evident on radar throughout August corresponded with fall migration departures (Hamel 1992, Brown 1997). In the southeastern United States, Purple Martins often depart for South America in early August (Hamel 1992).

Although the roost exhibited a seasonal pattern of growth and decline consistent with premigratory assembly, large daily fluctuations in TRP were evident. The accuracy of our TRP estimates depended on the following assumptions: (1) departures and arrivals were equally distributed around the roost, (2) each bird was counted only once during a survey, and (3) birds did not switch among roosts. The annular patterns from radar and uniform flight tracks over the observation point indicate that the first two assumptions probably were met for most morning departures, although some daily variation was likely. In contrast, the large variability and directional bias of evening flights and the lack of relationships between morning and evening counts indicate that the birds did not return to the roost in a uniform manner, and at least early in the evening some birds were counted multiple times. Thus, our evening counts likely did not provide an accurate estimate of the number of martins at the roost on a daily basis.

Another potential source of variation in TRP is movement of birds among roosts. During the present and subsequent (Russell et al. 1998) studies, we discovered another pre-migratory roost of martins 100 km west in Georgia and others within 230 km. Fluctuations in TRP through late July may reflect some switching of birds among roosts on a regional basis, while temporary increases in TRP late

in the season also could result from birds encountering the roost during migration from more northerly breeding or roosting sites. Likewise, birds migrating from Lake Murray probably encounter roosts along the Gulf coast (Russell et al. 1998). Although we believe our morning counts provide a good initial assessment of daily changes in TRP and maximum roost size, more accurate estimates will require monitoring roost populations on a regional basis. In part this may require rigorous, labor intensive ground surveys at multiple roost sites (e.g., Caccamise et al. 1983). However, with further refinements in methodology, WSR-88D radar may provide the potential to remotely monitor seasonal and annual changes in roost populations over large geographical areas (Russell and Gauthreaux 1998, Russell et al. 1998).

Why do Purple Martins assemble in premigratory roosts?-Large pre-migratory roosts of Purple Martins are neither a recent nor an isolated phenomenon. Wayne (1910), Stone (1937), and Anderson (1965) observed roosts reaching concentrations of at least 100,000, and a well-established roost at Lake Pontchartrain, Louisiana may support 200,000 birds (Rogillio 1989). Some roosts, including Lake Murray and a site in southern Oklahoma (Brown and Wolfe 1978) have been used by martins for 20 years or more (Russell et al. 1998). At least 30 additional major pre-migratory roosts are known to exist in the eastern United States (Russell et al. 1998). Enormous concentrations of roosting Purple Martins also have been documented on their wintering grounds (Oren 1980; Hill 1988, 1993).

Several selective advantages have been proposed for communal roosting behavior: premigratory assembly (Allen and Nice 1952, Michael and Chao 1973, Skutch 1989), reduced risk of predation (Lack 1968), more efficient thermoregulation (Williams et al. 1991), enhanced foraging ability through information exchange (Ward and Zahavi 1973, Brown and Brown 1996), and association with super-abundant food supplies or other diurnal activity centers (Caccamise and Morrison 1986, Caccamise 1993). Although the latesummer roosting habits of Purple Martins often are attributed to the need for pre-migratory assembly (Allen and Nice 1952), this seasonal pattern of roosting does not explain the benefits gained by gathering in a large communal assemblage for several weeks prior to migration (Caccamise et al. 1983, Brown 1997). Because the Lake Murray roost is on an island and at least 3 km from the lakeshore the birds likely have little threat from most predators or other disturbances; other large pre-migratory roosts of Purple Martins also are associated with bodies of water (Russell et al. 1998). Additionally, the anti-predator benefits of roosting should reach their maximum value at relatively small population sizes (e.g., < 1000; Pulliam 1973). Although roost advertising is evident in the pre-settling flight behavior of Purple Martins, the omnidirectional departures of the birds and their absence until evening make it unlikely that Lunch Island functions as an information center about local changes in food supply (Skutch 1989, Brown and Brown 1996, Brown 1997).

Our study has quantified aspects of the premigratory roosting behavior of Purple Martins that previously were known only from anecdotal accounts (see Brown 1997) or brief comments made during studies of nesting or immediate post-fledging activities (Allen and Nice 1952, Finlay 1971, Brown 1978). Future studies should focus on the costs and benefits of large pre-migratory roosts to Purple Martins and be conducted at scales sufficiently large to monitor spatial and temporal patterns of roosting on a regional basis (Caccamise et al. 1983, Russell et al. 1998). Studies employing radiotelemetry or other tracking methods also are needed to determine the daily and seasonal movements of individual martins, including whether individuals switch among roosts, or commute between roosts and diurnal activity centers (e.g., Caccamise and Morrison 1986, Caccamise 1993).

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